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To cite this article: J. Daisy Kaplan, Kelly Melillo-Sweeting & Diana Reiss (2017): Biphonal calls in Atlantic spotted dolphins (*Stenella frontalis*): bitonal and burst-pulse whistles, *Bioacoustics*, DOI: 10.1080/09524622.2017.1300105

To link to this article: <http://dx.doi.org/10.1080/09524622.2017.1300105>



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Biphonal calls in Atlantic spotted dolphins (*Stenella frontalis*): bitonal and burst-pulse whistles

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ABSTRACT

Biphonation, the simultaneous production of two sounds by a single animal, is found in the vocalizations of a range of mammalian species. Its prevalence suggests it plays an important role in acoustic communication. Concurrent vocal and behavioural recordings were made of Atlantic spotted dolphins (*Stenella frontalis*) off Bimini, The Bahamas. **The occurrence of two types of biphonal signals is reported: burst-pulse whistles with combined tonal and burst-pulse elements, and bitonal whistles.** Biphonal whistles are rarely described in reports of dolphin acoustic repertoires, but were common in these dolphins: of all whistles analysed ($n = 1211$), 26.84% were burst-pulse whistles and 4.71% were bitonal whistles. A subset of whistles ($n = 397$) were attributed to dolphins of specific age classes, and used to compare prevalence of biphonation across age. Biphonation occurred in 61.54% of sexually mature and 48.32% of sexually immature dolphins' whistles. Sexually immature dolphins emitted more burst-pulse whistles than older dolphins: 44.13% of sexually immature dolphins' whistles were burst-pulse whistles, while 15.38% of adult whistles were burst-pulse whistles. Bitonal whistle production was more prevalent in sexually mature dolphins: 41.03% of adult whistles were bitonal, while only 4.19% of sexually immature dolphins' whistles were bitonal. The prevalence of a biphonal component in specific repeated, stereotyped whistle contours suggests that these acoustic features could be important components of contact calls, or signature whistles. The biphonal components of spotted dolphin whistles may serve to convey additional information as to identity, age or other factors to conspecifics.

ARTICLE HISTORY

Received 3 May 2016

Accepted 9 February 2017

KEYWORDS

Biphonation; spotted dolphin; *Stenella frontalis*; whistle; non-linear phenomenon

Introduction

Biphonation, the simultaneous production of two independent frequencies (Wilden et al. 1998), is widespread in mammalian (Wilden et al. 1998; Tyack & Miller 2002) and avian vocalizations (Nowickil & Capranica 1986; Suthers 2001; Zollinger et al. 2008). Biphonal signals have been reported in cetaceans (Tyack & Miller 2002), canids (Volodin & Volodina

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Supplemental data for this article can be accessed here [<http://dx.doi.org/10.1080/09524622.2017.1300105>].

2002; Schneider & Anderson 2011), manatees (Mann et al. 2006), primates (Riede et al. 2007), birds (Aubin et al. 2000), and fish (Rice et al. 2011). The prevalence of biphonal calls in the acoustic repertoires of a wide range of vertebrate species suggests they may play an important role in communication. The addition of a second, simultaneously produced element in a call may enhance communication by conveying information such as motivation or status (Wilden et al. 1998) and may also serve to enhance individual recognition (Wilden et al. 1998; Aubin et al. 2000; Fitch et al. 2002; Volodin et al. 2006 and Volodina et al. 2006). The king penguin (*Aptenodytes patagonicus*), for example, relies on biphonation in its contact calls to encode individual identity (ID; Aubin et al. 2000).

Two well-studied examples in which the addition of a second element in a call can convey additional information beyond ID are the killer whale (*Orcinus orca*) and the dhole (*Cuon alpinus*). Both species produce biphonal calls comprised of simultaneously produced low- and high-frequency components that, when combined, may provide information on both directionality and identity (Volodin et al. 2006; Filatova et al. 2013). The high-frequency squeak of the dhole contains information on individual identification, while the low-frequency yap contains information on the orientation of the caller. Combined, the biphonal yap-squeak may provide cues to the receiver about both ID and orientation of the dhole signaller (Volodin et al. 2006). In contrast, it is the high-frequency component of the killer whale biphonal call that has strong directionality, with greater relative energy as the animal is moving towards a source rather than away (Miller 2002). It is suggested that these calls function for group coordination (Miller 2002). Killer whale biphonal calls, which can propagate further than monotonal calls, are produced more frequently in multipod aggregations, while monophonic calls are produced at a higher rate in single-pod groupings (Foote et al. 2008; Filatova et al. 2009, 2013). This higher occurrence of biphonal calls in multipod aggregations suggests they may function in part as identifying calls containing information about pod membership and matriline affiliation (Foote et al. 2008; Filatova et al. 2009, 2013).

Additional examples of the social function of biphonal calls can be found in common chimpanzees (*Pan troglodytes*) and red wolves (*Canis rufus*). Chimpanzees employ biphonal pant hoots in social situations including dominance displays, food discovery and intergroup calling (Riede et al. 2004). Red wolves produce squeaks and wuhs, either as separate units or in combination as a squeak-wuh (Schneider & Anderson 2011). In one captive population, squeaks were produced most often when the wolves were oriented towards others, which, the authors suggest, may indicate a solicitation function, while wuhs were more common during social interactions. Squeak-wuhs occurred most often during penmate-play or when oriented towards neighbours (Schneider & Anderson 2011).

Biphonation has been recorded in the vocalizations of both toothed and baleen whales, including minke whales (*Balaenoptera acutorostrata*) (Gedamke et al. 2001), North Atlantic right whales (*Eubalaena glacialis*) (Tyson et al. 2007), Bryde's whales (*Balaenoptera edeni*) (Figueiredo & Simão 2014), bowhead whales (*Balaena mysticetus*) (Tervo et al. 2011), long-finned pilot whales (*Globicephala melas*) (Nemiroff & Whitehead 2009), short-finned pilot whales (*Globicephala macrorhynchus*) (Sayigh et al. 2013), and Risso's dolphins (*Grampus griseus*) (Corkeron & Van Parijs 2001). The few reports that suggest social functions of biphonal calls in odontocetes (toothed whales) include establishing contact and group cohesion in beluga whales (*Delphinapterus leucas*) (Vergara et al. 2010) and facilitating reunion with group members in narwhals (*Monodon monoceros*) (Shapiro 2006).

Two odontocete species in which biphonation has been more widely reported are the bottlenose (*Tursiops truncatus*) and spotted (*Stenella frontalis*) dolphins; both species produce burst-pulse whistles in which tonal and burst-pulse elements are combined. These burst-pulse whistles have been reported to be emitted more frequently by younger animals, and in specific social contexts that have been described as emotive, emotional, or excited states (Caldwell & Caldwell 1967; Reiss 1988; Herzing 1996, 2000). Blomqvist et al. (2005) reported a ‘play-fight signal,’ comprised of a short burst-pulse combined with or followed by a frequency modulated whistle, used by juveniles and sub-adults in one group of captive bottlenose dolphins. Reiss (1988) reported the production of ‘whistle-squawks,’ the simultaneous production of a whistle and pulsed component, by infant bottlenose dolphins during the first few weeks of development. Whistle-squawks were emitted during emotional situations such as prolonged separation from the mother (Reiss 1988). A community of Atlantic spotted dolphins in White Sand Ridge, The Bahamas, produce biphonal ‘excitement vocalizations’ – burst-pulses with overlapping, frequency modulated signature whistles (Herzing 1996). These vocalizations were most frequently produced by calves and were the calves’ predominant vocalizations in behavioural contexts of excitement or distress, such as intraspecific social behaviour or human presence in the water (Herzing 1996). These signals appeared similar to whistle-squawks reported by Caldwell and Caldwell (1967) and Reiss (1988), further supporting the view that there is an emotive aspect to these vocalizations (Herzing 2000). Whines were recorded during play in juveniles and calves within this same community of White Sand Ridge dolphins (Dudzinski 1998). In addition to state or context, the addition of a biphonal element may also enhance individual recognition in spotted dolphins; Bebus and Herzing (2015) noted that burst-pulse vocalizations occurred repeatedly in the signature whistles of some individuals in this community, and may be a key characteristic of these individuals’ signature whistles.

Although biphonal burst-pulse whistles have been reported in dolphins, there are only two reports of dolphins producing two simultaneous tonal sounds: a ‘two-voice signature whistle’ was reported from wild common bottlenose dolphins off the coast of Namibia (Kriesell et al. 2014), and a bitonal signature whistle was recorded from a bottlenose population off Sicily (Papale et al. 2015). Although there is a paucity of evidence specifically of bitonal whistles in dolphins, our observations of the production of bitonal whistles by several different individual dolphins in a spotted dolphin community in The Bahamas suggest that bitonal whistles in dolphins may be more common than previously thought.

In the present study, we report the occurrence of two types of biphonal signals in Atlantic spotted dolphin vocalizations – burst-pulse whistles in which tonal and burst-pulse elements are combined, and bitonal whistles. The production of biphonal whistles are compared across age classes. The prevalence of specific whistle types and possible social functions are discussed.

Method

Study population and study site

A community of wild Atlantic spotted dolphins (*S. frontalis*) off Bimini, The Bahamas, was observed. This group is estimated to consist of approximately 120 animals with a 2:1 female to male sex ratio (however, approximately 30% are of unknown sex) (Melillo-Sweeting et al. 2014). This study group is habituated to boats and snorkelers due to interactions with

long-term commercial swim-with-dolphin and scientific research programmes (Melillo et al. 2009). This allows successful collection of underwater observations, including whistle recordings from individuals and social groups in close proximity to a researcher. A further advantage is that these dolphins reside in shallow waters with excellent visibility: underwater visibility ranges from 6 to 30+ m, depending on the weather and tide, and water depth is 3.5–12 m.

Data collection

Recordings of vocalizations and behaviour were collected over a total of 10 weeks during the summers of 2009 through 2013. Comparisons between years were not made in this study, so all recordings were treated as a single data-set. The study area off Bimini was accessed using a 19.8 m live-aboard sailboat, a 12.8 m Hatteras motor boat, or a 10.9 m Dakota motor boat. Boat surveys were undertaken from the sailboat 3–5 days per week for 10 h per day, and in the Hatteras 5 days per week for 5–6 h per day. Additional morning surveys were conducted in the Dakota 1–2 days per week for 3–4 h per day.

Concurrent video and acoustic recordings were captured by a researcher (JDK) with an HD/Mini-DV Canon HV30 video camera encased in a custom designed and built underwater housing (The Sexton Company LLC) with SQ26–05 hydrophone input (Cetacean Research Technology) and either an M-Audio MicroTrack II or a TASCAM DR-05 recording system. During some trips, acoustic recordings were collected with a SQ26–05 hydrophone and M-Audio MicroTrack II recording system by a researcher (DR) on board the research vessel. This hydrophone was suspended over the side of the vessel and lowered to a depth of ~1.8 m. The M-Audio MicroTrack II and TASCAM DR-05 were set at WAV encoder, 24 bits. The SQ26 hydrophone had a recording bandwidth of 0.02–50 kHz, with a flat frequency response from 50 Hz to 32 kHz (± 3 dB) and a sensitivity of -169 dB, re 1 V/ μ Pa. Recordings were sampled at a rate of 96 kHz, providing a Nyquist frequency for all recordings of 48 kHz. Student research assistants recorded supplemental video and took photographs that were later compared to photo identification (ID) catalogues in order to age, sex and identify individual dolphins.

Encounters were defined as in-water observations lasting a minimum of one minute during which time at least one dolphin was within visual range of the researcher, or if data were collected from on-board the vessel, if dolphins were visible from the surface within 30 m of the boat and remained within a 30 m vicinity for a minimum of one minute. If more than one encounter occurred on the same day, the encounters were considered distinct if at least one hour lapsed between sightings (including both surface and underwater sightings), or if all or most of the dolphins present in the new encounter were not present in the previous encounter.

Data were collected using underwater focal follows (Altmann 1974) and continuous recordings as described in Kaplan and Connor (2007). Focal follows were limited to four minutes in length or less in order to increase the number of animals sampled per encounter. The first focal follow of the week was the individual dolphin closest to the researcher upon the videographer's entrance into the water. The second focal dolphin was the next dolphin closest to the researcher, and so on. If a group was comprised of individuals that had been focal animals that week and individuals that had not been focal animals that week, priority was given to an individual that had not been a focal follow. If all individuals

within a group had been subjects of a focal follow during a particular week, priority was given to the animal that had been followed for the least amount of time. Focal follows were approximately four minutes in length, unless the dolphin/dolphins left the vicinity of the videographer for more than 30 s prior to reaching the four-minute mark, in which case another focal animal was chosen.

The behavioural states, sexes, IDs and ages of the dolphins in each encounter were noted. Behavioural states were defined as people-oriented, affiliative-social, escalated-social, foraging, travel, socio-sexual, aggressive, solitary and parental/alloparental (see Appendix 1 for descriptions of behavioural states). Sex was determined by observation of the genital slit, observation of a penis, repeated observation of a nursing calf, or observation of the repeated presence of a dependent calf. Dolphins were classified into one of five age classes based on amount of spotting (Herzing 1997). Dolphins were individually identified based on unique spotting patterns, scars, and nicks in their flukes, dorsal fins, and pectoral fins, and, when possible, were matched to the dolphin ID catalogue for confirmation of sex and age. Class II and younger Class III dolphins have very few spots, if any, requiring IDs to be based on permanent scars and fin notches, if present. However, 'rake marks,' temporary, thin white scars resulting from another dolphin biting or scraping the dolphin with its teeth, can be used as short-term identifying features; in this study, rake marks were used to distinguish and ID Class II and young Class III dolphins that lacked other identifying features within an encounter and across encounters that occurred within a day of each other. These identification techniques (amount of spotting, spotting patterns, notches, and scars) were utilized when assigning identifications and ages to vocalizing dolphins.

Data analysis of whistles

Raven Pro 1.5 TM acoustic analysis software (Cornell Laboratory of Ornithology, New York) was used to measure acoustic parameters of whistles and create spectrograms that could be visually categorized, with a fast Fourier transform size of 1024 points, an overlap of 50%, and using an 890 sample Han window. Whistles were used for analysis if they had a good signal-to-noise ratio in which the spectral contours were clearly visible in a spectrogram (Lammers & Au 2003; Papale et al. 2013).

Whistles were attributed to individuals based on bubble emission and/or proximity. If the onset of a whistle was concurrent with the emission of bubbles from a dolphin's blowhole, it was assumed that the whistle was emitted from that dolphin (McCowan 1995; McCowan & Reiss 1995; Herzing 1996; Fripp 2005). Whistles were also attributed to individual dolphins if there was only one dolphin in close proximity to the hydrophone (within four dolphin body lengths) and the whistle was loud (an amplitude of at least 99 dB), indicating the whistler was in close proximity.

In cases in which we were not able to individually attribute whistles to specific dolphins based on their proximity or bubble emission, if all dolphins in the encounter were in the same age class, we assigned whistles recorded in that encounter to that age class. For example, in the 16 August 2012 encounter, there were only two dolphins present, and both dolphins were Class V adults. We therefore considered all whistles from this encounter to be Class V dolphin whistles.

Dolphins were pooled into two age categories to compare whistles across ages: 'sexually immature' (calf/Class II and juvenile/Class III) and 'sexually mature' (young adult/

Class IV and adult/Class V) dolphins. This pooling of Class IV and V dolphins was necessary because our small sample size would have prohibited a robust comparison between Class IV and V dolphins. The amount of spotting which distinguishes Class II from Class III younger dolphins (Herzing 1997) was not always visible in video footage (due to proximity to the camera and/or water clarity), thus many of the older Class II and the younger Class III dolphins were difficult to assign to a Class II or III age category based on this spotting criteria. We therefore pooled all Class II (calf) and Class III (juvenile) dolphins together into the ‘sexually immature’ dolphin category. Whistles were then compared between two age groups: ‘sexually immature’ and ‘sexually mature’ dolphins. Dolphins’ whistles were placed into the appropriate age category at the time of each recording; as such a given individual’s

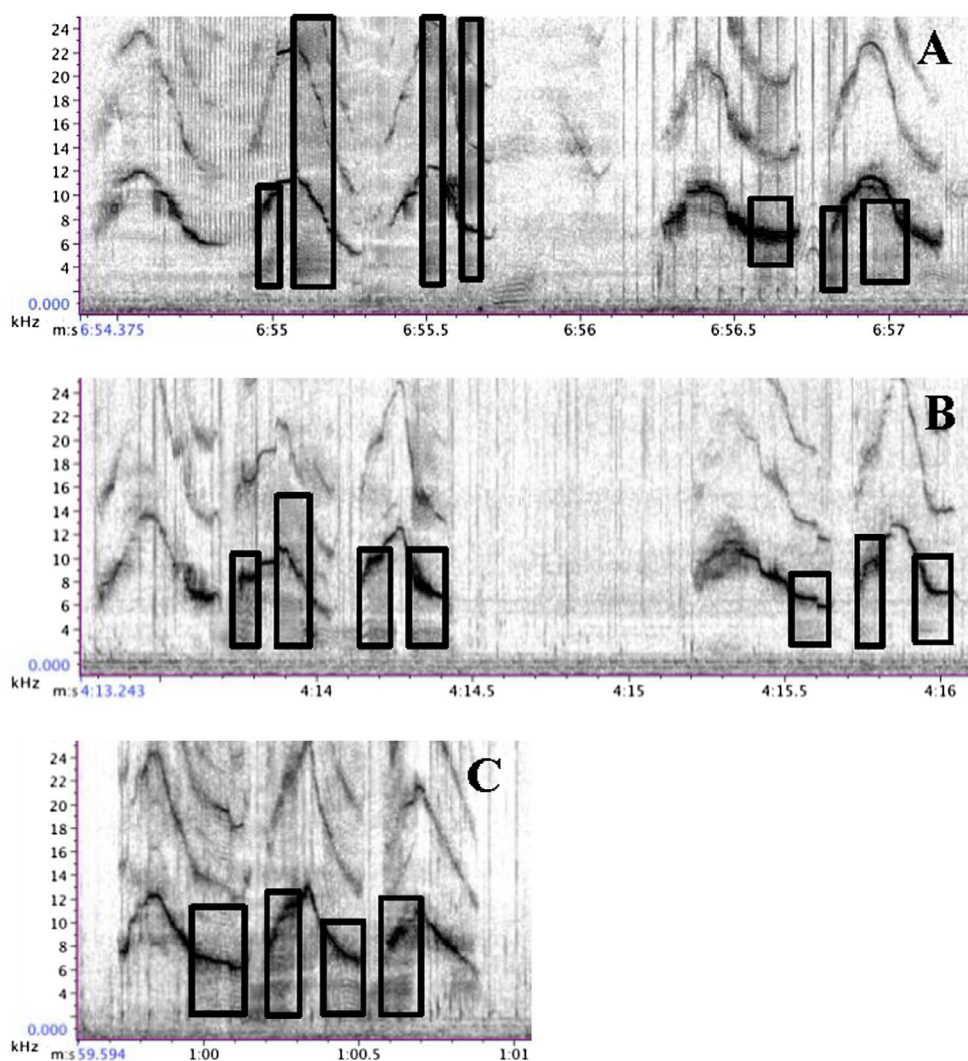


Figure 1. Examples of whistle type 15 with a simultaneously produced burst-pulse component.

Notes: (A) Whistle type 15 recorded in August of 2010. (B) Whistle type 15 recorded in June of 2011. (C) Whistle type 15 recorded in August of 2012, produced by ID #93. ID #93 was present in the other encounters as well, but no whistles could be identified to individual dolphins. Boxed areas indicate burst-pulse components.

whistles could be counted as whistles produced by a ‘sexually immature’ or ‘sexually mature’ dolphin depending on the age of the dolphin at the time of recording. No Class I (neonate) dolphins were observed in this study, so this age class was not included in any comparisons.

Vocalizations were categorized into types based on whistle contour by JDK (Janik & Slater 1998). Occurrence of biphonation was detected by simultaneously listening to the recordings while visually inspecting spectrograms (McCowan & Reiss 1995); confirming biphonation both acoustically and visually reduced the chance that a biphonal whistle would be missed or incorrectly classified as such. Two types of biphonation were classified: burst-pulse whistles and bitonal whistles. A burst-pulse whistle is defined in this study as a whistle with an overlapping, simultaneously occurring, burst-pulse component. A bitonal whistle is defined in this study as a signal comprised of two simultaneously occurring, distinct, nonparallel fundamental frequencies with no simple ratio relating them (Tyson et al. 2007).

When scoring biphonal whistles, one of two criteria was used to determine if the whistle was comprised of two simultaneously produced signals emitted from the same dolphin rather than two signals produced by two different dolphins. The first criterion was the stereotyped placement of a second component relative to a whistle contour. Many whistles that were recorded had stereotyped contours and were assigned to a whistle type. Several whistle types had an overlapping tonal or burst-pulse component that was produced in a characteristic temporal location in a large portion of the whistles recorded, across more than one encounter and/or on more than one day (Figures 1–4). In the case of bitonal whistles,

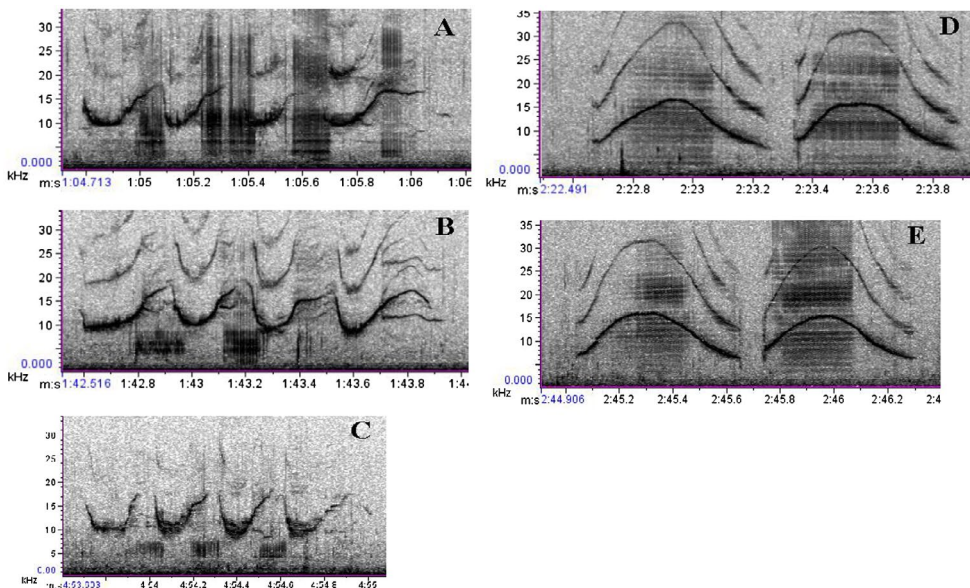


Figure 2. Examples of burst-pulse whistle types 9 and 24.

Notes: (A) Whistle type 9 was recorded in 2010 from ID #84 (Class III juvenile female). This whistle type was recorded 26 times (although not positively attributed to an individual all times) and contained a burst-pulse component in 73% of the occurrences. (B) Whistle type 9 recorded in 2012 from ID #84. (C) Whistle type 9 recorded in 2011 – not attributed to an individual, but ID #84 was present in this encounter. (D) and (E) Whistle type 24 was recorded 25 times and contained a burst-pulse component in every recorded occurrence. This whistle type was produced by ID #95 (Class III male) 23 times in one encounter. Sound files for examples A, C, and D are included as supplemental online material.

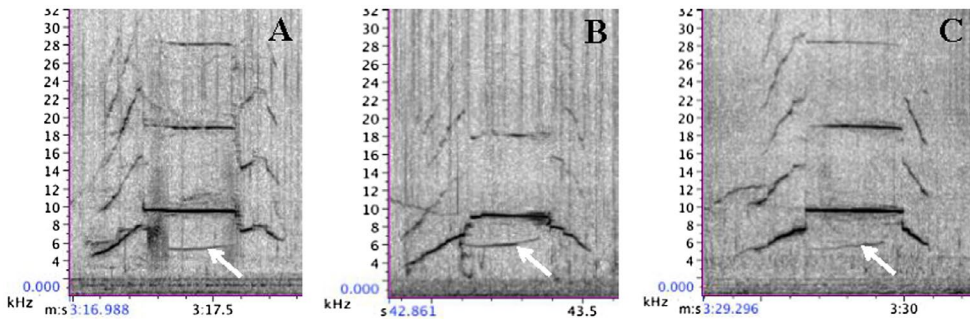


Figure 3. Examples of bitonal whistle type 8.

Notes: (A) Whistle type 8 recorded in 2012 from ID #48 (Class V female). (B) and (C) Whistle type 8 recorded in the same encounter – ID #48 was present but whistles could not be attributed to an individual dolphin. The low-frequency component is indicated by arrows. Note that in Figure 3B, the low-frequency element immediately preceding the element indicated by the arrow is probably another dolphin. The sound file for example C is included as supplemental online material.

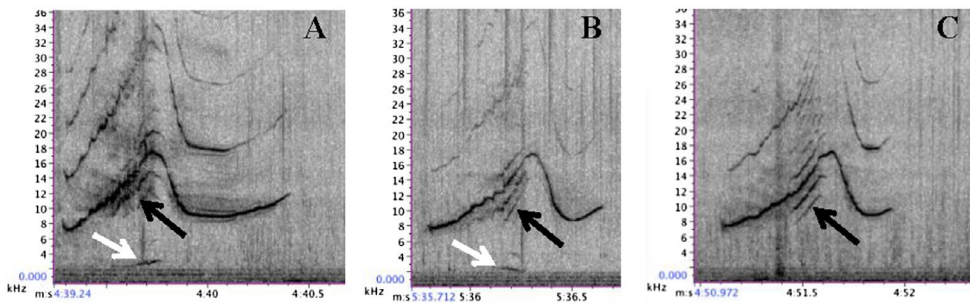


Figure 4. Examples of bitonal whistle type 11.

Notes: Whistle type 11 was recorded 27 times across 5 encounters, 42% were bitonal. (The other samples had low signal-to-noise ratio.) Nine type 11 whistles were produced by ID #70 (Class V female) during one encounter. (A) and (B) Type 11 produced by ID #70. The low-frequency component is indicated by white arrows. Subharmonics are indicated by black arrows. (C) An example of a monophonic whistle produced by ID #70 without a low-frequency component. Subharmonics indicated by the black arrow. The sound file for example A is included as supplemental online material.

the second, tonal component had a characteristic, stereotyped contour. This second element was shorter in duration, lower in frequency, began after the onset of the first component, ended before the end of the first component and was less complex in structure. The contour of the second component was either a relatively flat contour, a rise, or a slight fall (Figures 3–5). It is unlikely and improbable that two different dolphins synchronized the production of these two specific stereotyped contours with such precise timing across a long period of time in a single encounter or across multiple encounters across multiple years. Whistle contours that had a stereotyped placement of a second, stereotyped component were therefore counted as biphonal whistles, and it was assumed that both sounds were most likely produced by the same dolphin. The second criterion was proximity; if both components (two tonal sounds in the case of bitonal whistles, or a burst-pulse component and whistle in the case of burst-pulse whistles) occurred simultaneously, were both loud in amplitude (greater than 99 dB), and only one dolphin was in close proximity to the hydrophone (within four dolphin body lengths), it was assumed that both components of the whistle were produced by the same dolphin.

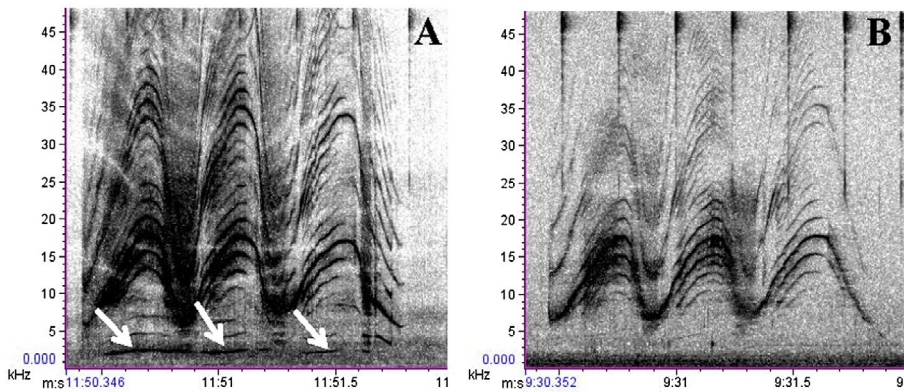


Figure 5. Examples of bitonal whistle type 6.

Notes: (A) Whistle type 6 recorded from dolphin ID #10 (a Class IV female). The low-frequency components are indicated by arrows. (B) An example of 6 without the lower frequency second tonal component, recorded from dolphin ID # 10 during the same encounter. Sound files for examples A and B are included as supplemental online material.

Results

Whistles were analysed from 693 min of recordings. These recordings were collected over 24 days and across 39 different encounters during 2009–2013. The groups ranged in size from 1 to more than 30 dolphins, and were comprised of a mix of juveniles, adults and calves.

A total of 1211 whistles with good signal-to-noise ratio were analysed for the occurrence of biphonation. **Biphonation was prevalent in spotted dolphin whistles in this community: 31.54% ($n = 382$) of all whistles analysed were biphonal. Burst-pulse whistles were more common than bitonal whistles: 26.84% ($n = 325$) of all whistles analysed were burst-pulse whistles, while only 4.71% ($n = 57$) were bitonal.** Five of these 382 whistles had both burst-pulse and bitonal elements, so are included in both the burst-pulse whistle and bitonal whistle counts.

We were able to attribute 397 whistles to a specific age class of dolphin, and of these 397, we were able to attribute 167 whistles to individual dolphins within each age class. This subset of 397 whistles was used to examine the production of biphonation in dolphins across age classes. Thirty-nine whistles were attributed to sexually mature dolphins: 13 whistles were attributed to 4 different Class IV young adults and 26 whistles were attributed to 4 different Class V adults. The majority of these whistles, 358 out of 397, were attributed to 14–17 different sexually immature (Class II and Class III) dolphins. A range of 14–17 is given because some of the calves to which we attributed whistles did not have permanent scars or distinct spot patterns that could be used to identify them. We were able to identify these calves within an encounter or in encounters occurring within two days of each other by ‘rake marks,’ or temporary white scars. Since these scars only last for two or three days, we could not determine with certainty whether some calves from two different encounters further than two days apart were the same calf or two different calves.

Biphonation occurred in 48.32% of the whistles of sexually immature dolphins and 61.54% of the whistles of young adults and adults. Younger dolphins emitted significantly more burst-pulse whistles than older dolphins did, $\chi^2(1) = 11.99, p < .001$: 44.13% ($n = 158$) of Class II and III whistles were burst-pulse whistles, while 15.38% ($n = 6$) of adult whistles were burst-pulse whistles. There was a significant difference between age classes in the

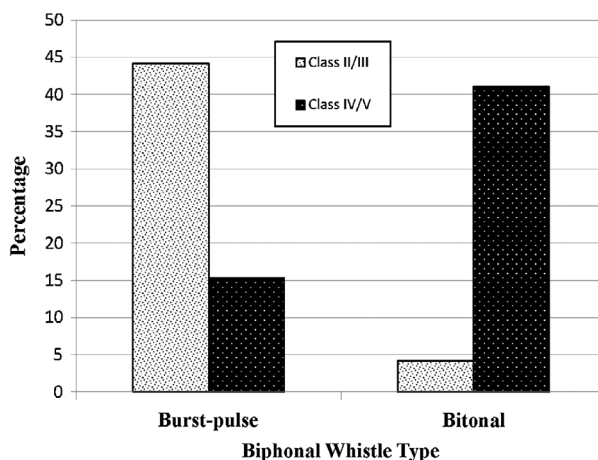


Figure 6. Comparison of biphonation in sexually immature and sexually mature dolphins.

Notes: Biphonation occurred in 48.32% ($n = 173$) of the whistles produced by sexually immature (Class II/III) dolphins and in 61.54% ($n = 24$) of young adult and adult (Class IV/V) dolphins. Sexually immature dolphins emitted more burst-pulse whistles than older dolphins, and older dolphins emitted more bitonal whistles than did sexually immature individuals.

production of bitonal whistles, $\chi^2(1) = 81.26$, $p < .001$: 41.03% ($n = 18$) of adult whistles were bitonal, while only 4.19% ($n = 15$) of Class II and III whistles were bitonal (Figure 6). Sample sizes were not large enough to compare whistle use between Class IV and Class V dolphins. Because only a small number of whistles were attributed to males, comparisons in whistle production between sexes were not made.

We conducted a second, more conservative analysis which included whistles attributed to a dolphin based on bubble stream production current with vocalizations (an established method of identifying vocalizing dolphins), and excluded the 23 vocalizations that were attributed to dolphins based on proximity (a method of identifying dolphins that is not as frequently used in the literature). In cases in which no bubble streams were observed, if all dolphins in the encounter were of the same age class, the whistle was attributed to that age class. Results were similar to those found in the first analysis. This second analysis included 374 whistles; 28 of these whistles were produced by 7 adult (Class IV and V) dolphins, and 346 were produced by 14–17 sexually immature (Class II and III) dolphins. Biphonation occurred in 47.69% of Class II and Class III whistles and 64.29% of adult whistles. Younger dolphins emitted more burst-pulse whistles than older dolphins: 43.35% ($n = 150$) of Class II and III whistles were burst-pulse whistles, and 21.43% ($n = 6$) of adult whistles were burst-pulse whistles. As in the first analysis, we found a marked difference between age classes in the production of bitonal whistles: 42.86% ($n = 12$) of adult whistles were bitonal, while only 4.33% ($n = 15$) of Class II and III whistles were bitonal.

Burst-pulse whistles

Six of the 36 whistle types recorded typically appeared as biphonal, burst-pulse whistles: whistle types 9, 12, 15, 24, 27 and 28. These whistle types were recorded multiple times, and were often produced by specific individuals (Table 1). Examples of these burst-pulse whistles are given in Figures 1 and 2. Sound files for examples of whistle types 9 and 24

Table 1. Frequency of occurrence of burst-pulses in whistle types and IDs of dolphins that produced them.

Whistle type	BP/total	Dolphin IDs
9	19/26	#84 (juvenile F)
12	43/80	1 or more calves
15	31/41	#93 (juvenile F)
24	25/25	#95 (juvenile M)
27	12/14	C3D (juvenile F)
28	3/3	#64 (young adult M)

Notes: BP/total refers to the number of times this whistle type contained a burst pulse component out of the total number of times this whistle was recorded. Only whistles with high signal-to-noise ratio are included in this count. Dolphin IDs are dolphins that were identified as producing this whistle type. Age class and sex of the dolphin IDs are noted in parentheses.

are included as supplemental online material. Out of the entire set of 1211 whistles, other whistle types also contained burst-pulse components, but were only recorded a few times and were not attributed to individuals, so were not included in the analysis of individual dolphin production of whistle type. **The occurrence of burst-pulse whistles was not context-specific; several different burst-pulse whistle types were recorded during affiliative-social, escalated-social, people-oriented and solitary behavioural contexts.** Descriptions of these specific whistle types, the dolphins that produced them, and the social context in which they were produced follow.

Whistle type 9 was recorded 26 times, with a burst-pulse component in 73.08% of these whistles. This whistle was attributed to dolphin ID #84, a Class III juvenile female, in two separate encounters in 2010 and 2012 (Figure 2). This whistle type was also recorded in two additional encounters in 2011. No whistles could be attributed to individuals in these encounters, but ID #84 was present in both encounters. Both of these encounters were comprised of a group of three Class II/III females.

Whistle type 12 was recorded 80 times in 6 separate encounters over 4 years, and contained a burst-pulse component in 53.75% of the occurrences. All 44 of the 80 whistles that were attributed to individuals were attributed to a calf or young juvenile that was too young to be permanently catalogued due to lack of permanent scars or distinct spot pattern. This could have been the same dolphin or different dolphins.

Whistle type 15 was recorded 41 times and contained a burst-pulse component 75.61% of these times (Figure 1). This whistle was attributed to dolphin ID #93, a young Class III female, across multiple encounters and multiple years. ID #93 was first recorded producing this whistle when she was a Class II dolphin, but she was classified as a Class III female by the end of the study.

Whistle type 24 was recorded 29 times and contained a burst-pulse component in every example (Figure 2). This whistle type was produced by dolphin ID #95, a Class III male, 23 times in one encounter in 2011. The whistle was recorded in four other encounters in 2010, 2011, 2012 and 2013, but was not attributed to an individual dolphin in these encounters. ID #95 was one of four dolphins present in the 2010 encounter, and was also present in the 2012 and 2013 encounters. It could not be determined whether ID #95 was present or absent in the other 2011 encounter.

Whistle type 27 was recorded 14 times across two encounters, and contained a burst-pulse component in 85.71% of the whistles recorded. This whistle was produced at least three times by dolphin C3D, an uncatalogued Class III female, in one encounter in 2011. This whistle type was recorded in another encounter one month later in 2011. No whistles

were attributed to individuals in this later encounter, but the group in the second encounter was comprised of three Class II/III females, one of which was dolphin C3D.

Whistle type 28 was recorded three times during two separate encounters, and contained a burst-pulse component in all examples. All three whistles were attributed to dolphin ID #64, a Class IV male. One of these encounters was a mixed-species encounter, with both bottlenose and spotted dolphins.

Bitonal whistles

Bitonal whistles were comprised of two tonal components – a higher frequency component and a lower frequency component. The higher frequency component was produced alone or in combination with the lower frequency component. The higher frequency component was a frequency modulated whistle that was between 1.58 and 25.09 kHz. The mean low frequency of these whistles was 5.58 kHz (SD = 1.66 kHz, range = 1.58–9.68 kHz), the mean high frequency was 17.12 kHz (SD = 3.51 kHz, range = 9.24–25.09 kHz), and the mean duration was 1.11 s (SD = 0.31 s, range = 0.56–1.97 s). The lower frequency component was between 0.70 and 13.85 kHz. This component was much shorter in duration, with a mean duration of 0.19 s (SD = 0.08, range = 0.05–0.49 s), and in some whistles was repeated during production of the first element (Figure 5). The lower frequency component tended to be flatter, with one or no inflections.

Of the 36 whistle types recorded, six whistle types were often found to have two tonal components: whistle types 3, 5, 6, 8, 11 and 12. Some of these whistle types, though usually biphonal in form, also appeared as monophonic whistles (Figures 4 and 5). These bitonal whistles, like the burst-pulse whistles, did not appear to be context-specific: bitonal whistles were recorded during affiliative-social, escalated-social, people-oriented and solitary behavioural contexts. These six whistle types were recorded multiple times, and were often produced by specific individuals (Table 2). Examples of bitonal whistles are given in Figures 3–5. Sound files for examples of whistle types 6, 8 and 11 are included as supplemental online material. Descriptions of these six whistle types, the dolphins that produced them, and the social context in which they were produced follow.

Whistle type 3 was recorded three times during one encounter. Two out of three of these whistles had a second, lower frequency component. This second component was a short rise below 7.6 kHz. All samples of whistle type 3 were produced by dolphin ID #35, a Class IV female, during this encounter. This encounter began with two juveniles circling swimmers. These two juveniles left, and ID #35 remained. She alternated between circling swimmers and solitary swimming. She appeared pregnant at the time of this encounter.

Table 2. Frequency of occurrence of bitonal components in whistle types and IDs of dolphins that produced them.

Whistle Type	BiT/Total	Dolphin IDs
3	2/3	#35 (young adult F)
5	11/20	Old Whitey (adult, unknown sex)
6	23/34	#10 (young adult F) and 1 or more calves
8	6/12	#48 (adult F)
11	8/19	#70 (adult F)
12	4/80	1 or more calves

Notes: BiT/total refers to the number of times this whistle type contained a second tonal component out of the total number of times this whistle was recorded. Only whistles with high signal-to-noise ratio are included in this count. Dolphin IDs are dolphins that were identified as producing this whistle type. Age class and sex of the dolphin IDs are noted in parentheses.

Whistle type 5 was recorded 20 times across three encounters. Most whistles had low signal-to-noise ratio, so the presence of a bitonal component could not always be determined. Eleven out of 20 of these whistles had a low-frequency rise component under 13.90 kHz. Six of these whistles were attributed to 'Old Whitey,' a Class V dolphin, sex not known, during one encounter. Included in this encounter were three or four calves and juveniles engaged in social interaction with each other. Old Whitey was stationed on the outskirts of this group during this encounter.

Whistle type 6 was recorded 34 times across 5 encounters, and was produced by two or more different dolphins. A second, simultaneously produced, flat tonal element below 5 kHz was present in 23 of these 34 whistles (Figure 5). This whistle was recorded once in an encounter in 2011 from a group comprised of dolphin ID #87 (a Class III female) and two unidentified Class II/III dolphins. This contour was produced 14 times by a Class II calf in 2 encounters in 2012; one encounter was with a group of 3 calves and young juveniles, and one encounter was with a group of over 30 dolphins. The calves that the whistles were attributed to in these two encounters may have been the same calf or two different calves. Whistle 6 was recorded four other times in an encounter in 2013 from a group comprised of eight dolphins of mixed ages. ID #87 was part of this group. In an encounter three days later, whistle 6 was produced by dolphin ID #10 (a Class IV female) at least six times, once without the second tonal component (Figure 5). The group in this encounter was comprised of two dolphins: ID #10 and ID #87. These two dolphins were engaged in mutual object play, carrying clumps of sargassum on a pectoral fin, dorsal fin, rostrum, or fluke, and then dropping it for the other dolphin to pick up.

Whistle type 8 was recorded 18 times across 5 encounters (Figure 3). Six of these whistles were very faint, so it was not possible to determine presence of a second tonal component. In the other 12 whistles recorded, six had a simultaneously produced lower tonal rise component. This lower component was below 7.6 kHz. In one encounter this whistle was attributed to dolphin ID #48 (a Class V female). This encounter began with five dolphins of mixed ages. Three of the dolphins left and two Class V females, ID #48 and ID #70, remained. The two alternated between affiliative-social behaviour, people-oriented behaviour, and solitary swimming. ID #70 produced a bitonal whistle during this encounter, whistle type 11, described below. ID #48 was present in another encounter during which whistle type 8 was recorded, but no whistles in that encounter could be attributed to an individual dolphin.

Whistle type 11 was recorded 27 times across 5 encounters. Eight out of 19 of these whistles had a second tonal element under 3.70 kHz (Figure 4). This second tonal element was either flat, or had a slight rise or fall. The other whistles were faint, with a low signal-to-noise ratio, so it is possible that more of these whistles were bitonal, but that the lower component was undetectable because of low signal-to-noise ratio. Nine of these type 11 whistles were produced by ID #70 (a Class V female) during one encounter. Eighteen of these whistles were recorded from mixed-age groups of dolphins but could not be attributed to individual dolphins.

Whistle type 12 was recorded 80 times in 6 separate encounters. Only four of these whistles contained a second, brief, low-frequency flat or slight rise component. All four of these bitonal whistles were recorded from the same encounter, and were attributed to one or more Class II calves.

Discussion

Biphonation frequently occurs in the whistles of Atlantic spotted dolphins observed off Bimini, The Bahamas. Biphonal whistles comprised over 30% of all whistles recorded in this study. The regular occurrence of a biphonal burst-pulse component or simultaneously produced second tonal component in specific repeated, stereotyped whistle contours, some of which were attributed to individual dolphins, suggests that burst-pulse and bitonal components could be important features that convey identity information in what may be individual contact calls, or 'signature whistles.' We observed differences in the production of burst-pulse and bitonal whistles between age groups.

Burst-pulse whistles were produced more by younger dolphins than older dolphins in this study: 44.13% of calf and juvenile whistles were burst-pulse whistles, while less than 16% of adult whistles were burst-pulse whistles. Of all of the whistles attributed to individual adult dolphins, no whistles emitted by Class V adults contained burst-pulse components, while at least 11 of the 14–17 Class II and Class III dolphins recorded in this study produced burst-pulse whistles. Although the sample sizes were small for Class IV and Class V adult whistles, this suggests that burst-pulse whistles occur much more frequently in younger animals than in older animals. Bebus and Herzing (2015) suggest the addition of burst-pulse components may be an important feature of specific individual juvenile (Class III) dolphins' signature whistles in spotted dolphins observed on White Sand Ridge, a different area of The Bahamas.

Whistle-squawks, or whistles with overlapping burst-pulses, have been reported in prior studies in dolphins in states of distress or excitement (Caldwell & Caldwell 1967; Reiss 1988; Herzing 1996, 2000). A little more than half (55.85%) of the burst-pulse whistles recorded from Class II and III dolphins in this current study were produced during people-oriented states, and therefore the higher percentage of burst-pulse whistles recorded in younger Class II and III dolphins as compared to the older Class IV and V dolphins may be due in part to the tendency of younger animals to frequently swim close to and encircle researchers in the water while vocalizing. It remains unclear whether the burst-pulse component concurrent with whistle production in young spotted dolphins is an unintentional by-product of an excited vocal system, due to arousal and excitement, or an intentional component that adds potential information to the signal.

Notably, in the Bimini community of spotted dolphins there was a distinct age difference in the production of bitonal whistles recorded. Of those attributed to individual dolphins, 41.03% of the whistles produced by sexually mature dolphins were bitonal, while only 4.19% of whistles produced by calves and juveniles were bitonal. Whistles were attributed to eight adults, and seven of these eight adults produced biphonal whistles. Two adult Class IV males (ID # 64 and ID # 78) produced biphonal burst-pulse whistles. Only one whistle was recorded for male ID #78, however, so this result for ID #78 may not be representative. Five of the eight adults – two adult females, two young adult females, and one adult of unknown sex – produced bitonal whistles. The stereotypic nature of these repeated whistles could mean that these bitonal whistles are signature whistles. Bitonal signature whistles have been reported in bottlenose dolphins (Kriesell et al. 2014; Papale et al. 2015), so it would not be surprising to find bitonal signature whistles in spotted dolphins as well.

We speculate that the addition of a second, tonal element in what may be signature whistles could provide additional information about age and/or role. For example, adult Atlantic spotted dolphins have been observed 'babysitting,' or taking on alloparental roles

(Herzing 1996, 2015; Herzing & Elliser 2013), and a whistle with these elements that might provide cues to age or role could be highly advantageous.

Dolphin whistles also have directionality, as shown by Branstetter et al. (2013, 2012) and Lammers and Au (2003). These authors suggest whistle directionality may provide cues about the orientation and direction of movement of the signaller, aiding in coordinated group movement and cohesion (Lammers & Au 2003; Branstetter et al. 2012, 2013). Signals that convey information about orientation or direction of movement of the signaller would be beneficial in species such as dolphins that live in environments often visually restricted by factors such as water turbidity or the darkness of night. Dholes and killer whales produce biphonal calls which may provide additional cues that their monophonic calls lack, possibly conveying information about both direction and identity to the receiver (Volodin et al. 2006; Volodina et al. 2006; Foote et al. 2008; Filatova et al. 2009, 2013). The addition of a second component in Atlantic spotted dolphin whistles could function in a similar manner, providing additional information about directionality and identity.

It is possible that the two concurrent components in the burst-pulse whistles and bitonal whistles of spotted dolphins are produced by two different sound sources. Early studies described the bottlenose dolphin's ability to whistle and click simultaneously (Lilly & Miller 1961). Lilly (1962) reported that the bottlenose dolphin produced these signals with two different sound sources, tended to click with the left mechanism and whistle with the right, and could produce both sounds individually or together. Cranford et al. (2011) demonstrated that dolphins are capable of producing acoustic pulses or clicks with either their right or left set of phonic lips, and can generate sounds from these sets of phonic lips independently or simultaneously. Madsen et al. (2013) demonstrated that five bottlenose dolphins and a false killer whale could produce clicks and whistles simultaneously, usually producing clicks with the right set of phonic lips and whistles with the left. They suggested that dolphins could probably produce whistles with the right set of phonic lips as well, but do not usually do so (Madsen et al. 2013). In summary, these studies indicate that dolphins can click and whistle simultaneously from two separate sound sources. Biphonal signals have commonly been considered non-linear phenomenon in the cetacean literature, although biphonation could be considered a linear process if these two sounds are produced by two independent sources (Mann et al. 2006). It should be noted that in the physical acoustics literature the term nonlinear is reserved exclusively for systems which fail the superposition principle, namely that the sound produced by two sources is the sum of the sounds produced by either. 'Nonlinear' in this context would imply that the sources affect one another (Mindlin 2013), as would be the case if the two oscillators were coupled (Fitch et al. 2002), which is not a claim we can make in this paper.

It is not clear if the production of bitonal whistles is intentional, or a by-product due to the excitement or emotive level of the animals or other physiological or anatomical factors. Captive bottlenose dolphins are reported to produce non-stereotyped whistles at birth, and develop more stereotyped contours over the first year or two of their lives (Caldwell & Caldwell 1967; Reiss 1988; McCowan & Reiss 1995). The occurrence of bitonal whistles in older dolphins and burst-pulse whistles in younger dolphins may coincide with the development of vocal control or learning. This may account in part for why mainly older, adult dolphins produced bitonal whistles. However, one or two younger animals produced bitonal type 6 whistles. A Class II dolphin producing the type 6 whistle in one encounter was estimated to be at least 3 years old, based on the appearance of spots on the rostrum.

The Class II dolphin producing the type 6 whistle in an encounter two days later was too far from the camera to note rostrum spotting pattern, and may or may not have been the same Class II dolphin. Although burst-pulse whistles were produced primarily by sexually immature dolphins, it is unlikely that the burst-pulse component is only due to immaturity and a lack of vocal control, as many of these animals that produced burst-pulse whistles were well over 5 years old, and two of the animals were young adults. Furthermore, burst-pulse whistles have been reported in adults in other studies (e.g. Caldwell & Caldwell 1967; Herzing 1996, 2000; Blomqvist et al. 2005).

This study faced some limitations; sample sizes were not large enough to compare the production of biphonation between sexes, or between young adult Class IV and adult Class V dolphins. Also, the attribution of whistles to individuals remains challenging and thus the number of whistles for individual dolphins was low. With a larger data-set, comparisons can be made that will further elucidate how biphonal calls function within spotted dolphin societies.

The prevalence of biphonation in the whistles in the current study group suggests that biphonation may play an important role in spotted dolphin acoustic communication signals, conveying information such as age and identity. Although there are a few descriptions of biphonal calls in dolphins comprised of simultaneously produced whistles and burst-pulse components, descriptions of bitonal whistles comprised of two *tonal* components are lacking in the literature, with the exception of one report of a 'two-voice' bitonal signature whistle recorded in a bottlenose dolphin population in Namibia (Kriesell et al. 2014) and a report of a bitonal signature whistle type in a bottlenose dolphin population in Sicily (Papale et al. 2015). When initially reviewing acoustic recordings of dolphin vocalizations, bitonal calls may be interpreted as being two concurrent whistles produced by two different dolphins. However, it becomes evident that the two tonal components are part of the same whistle when the same components occur simultaneously in a stereotypical pattern multiple times across multiple encounters and years. This provokes the question: are bitonal whistles present, but unnoticed, in other populations of dolphins, or are bitonal whistles unique to certain dolphin communities or populations? This question can only be answered with further investigation into repertoires of other populations.

Conclusion

Biphonation, the simultaneous production of two sounds, is a commonly occurring characteristic in Atlantic spotted dolphins observed off Bimini, The Bahamas. Biphonal components of whistles may provide additional cues as to identity in spotted dolphin whistles. Bitonal whistles are produced more frequently by adults than by sexually immature dolphins, while burst-pulse whistles are produced more often in younger than in older animals. Biphonal calls are produced by several different individuals in this population and the same individual may produce a particular whistle type both with and without a burst-pulse or tonal component. Biphonal components appear in several different whistle types and in particular, biphonation often occurs in repeated, stereotyped whistle contours, which may be individual dolphins' contact calls or signature whistles. Whether biphonation is used in other types of whistles as well remains unclear and a larger sample size of biphonal whistles will be needed to determine this.

Acknowledgements

This research was conducted under research permits granted by The Bahamas Environment, Science and Technology Commission and the Department of Marine Resources.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This research was supported by The Animal Behaviour Society Cetacean Behavior Award (JDK), CUNY Doctoral Student Research Grant #5 (JDK), CUNY Doctoral Student Research Grant #7 (JDK), The National Geographic Society Grant for Research and Exploration (DR), and the Hunter College Study Abroad Program (DR, JDK).

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Appendix 1.Behavioural states

Behavioural state	Description
Travel	Dolphin(s) moving in one direction at a moderate to fast speed for an extended period of time
Foraging	Dolphins chase fish at the surface, chase and then consume fish swimming in the water column, or scan and echolocate the ocean floor, and/or push their rostrums into the sand in an attempt to consume a fish buried in the substrate
People-oriented	Dolphins repeatedly circle people in close proximity (approximately two dolphin body lengths away). Circling is often accompanied by whistling. Dolphins dive down with people, while monitoring the position of the human that is diving down in close proximity to the dolphins
Parental/alloparental	Mother/calf or alloparental/calf interactions, including nursing, and/or observation of an older, supervising dolphin interacting with and tending younger dolphins (Herzing 1996)
Affiliative-social	Dolphins swim slowly, engaging in affiliative physical contact using their bodies, pectoral fins, and/or flukes, including engaging in behaviours such as petting and contact swimming
Escalated-social	Affiliative behaviours are combined with fast swimming and chasing. Occasional nipping, tail slapping and squawking may be observed. Behaviours that are considered aggressive, such as raking, tail-slapping, and squawking, are combined with contact swimming and synchronized surfacing with the same individuals towards which the aggressive behaviours are displayed
Socio-sexual	Affiliative behaviours are combined with genital buzzing and penis extrusion. Intromission and squawking might also be observed
Aggressive	An 'aggressive' state comprises rapid movements and one or more of the following behaviours: tail slaps, jaw claps, squawks, bubble bursts, and raking. An 'aggressive' state is distinguished from social or socio-sexual states in that there are little or no instances of slow swimming or affiliative tactile behaviours
Solitary	Only one dolphin is present. Dolphin is swimming slowly in no particular direction, and is not foraging, travelling, or displaying people-oriented behaviours